

CYTOTAXONOMY AND DISTRIBUTIONAL ECOLOGY OF
WESTERN NORTH AMERICAN VIOLETS

JENS CLAUSEN

During the years from 1932 to 1943 the chromosome numbers of violets from many natural habitats throughout western North America were determined. In some species determinations were made on plants from many populations. The present paper is a report on these studies. They were conducted in cooperation with my friend, the late Milo S. Baker of Santa Rosa Junior College, who made many trips through the western states and fixed plants in the wild when they were in early blooming stage. He also brought plants back to his garden at Kenwood, Sonoma County, California, and made other fixations there. Through many yeers this garden contained a remarkable collection of *Viola* species from out-of-the-way places which he treated with tender care.

Other western violets were collected and bud materials fixed by myself and David D. Keck on collecting trips throughout the western states, especially California. In the early years of the study some of these collections were grown in the greenhouses at the Department of Plant Biology of the Carnegie Institution of Washington. It soon became evident, however, that most of the wild species of the *Chamaemelanium* section of *Viola* were ill-adapted for cultural practices and were difficult to keep alive in the experiment garden at Stanford. Even in Baker's more favorable garden at Kenwood the *Chamaemelanium* violets were unable to survive for a longer period than two to four years. For these reasons the *Viola* project was primarily limited to the approaches of cytotaxonomy and distributional ecology.

Baker and I cooperated on the major taxonomic classification which was greatly aided by the chromosome numbers, by careful field studies and by study of specimens from about 14 herbaria throughout the country. The specimens were pooled for the study and annotated through 1936-1938. A complete list of these specimens was prepared and supplemented by impressions of leaves and flowers of critical specimens. The list and impressions were of great help in the study of the distributional ecology and morphology of the taxa and is deposited as documentation at the herbarium of the University of California, Berkeley.

It was agreed that Baker should write the taxonomic descriptions providing the nomenclature. The taxonomic papers (Baker, 1935-1960) were to be followed by a paper on the chromosome situation and its implications for classification.

At the 1935 meeting of the American Association for the Advancement of Science at St. Louis, Missouri, I gave a paper on the chromosomal distributional situation in the *Purpureae* and the *Nuttallianae* of the *Chamaemelanium* section. Eventually Baker (1949d) provided a tabular

list of the chromosome numbers of the various taxa, mentioning that the cytological work had been done by me. The proper bibliographical citation of these chromosome numbers is therefore Baker (1949).

In 1951 most of the chromosome numbers of the species were listed and diagrammed (Clausen, 1951), but the numbers were never documented by reference to the herbarium sheet or the locality where the plant was taken.

The purpose of the present paper is to provide the documentation and to integrate the field evidence with the cytological information and with the findings on the close relatives of our western violets from other parts of the world investigated by authors such as Gershoy and Miyaji. Gershoy in 1936 provided me with information on the sources of some of the plants he used in the determination of the chromosome numbers, and this information is also included in the listing (table 1). Unless otherwise stated the chromosome determinations are based on fixations made of bud materials from the plants growing in their natural habitats. When proper meiotic stages were unavailable mitotic divisions in the floral regions were successfully used for the counting of chromosomes.

CLASSIFICATION AND EVOLUTIONARY PATTERNS

In the chromosome list (table 1) the taxa are arranged alphabetically under sections, subsections (cenospecies), species, and subspecies. In the text the arrangement is ecologic-geographical, combined with cytological evidence in order to provide a background for an evolutionary understanding.

The genus *Viola* has many natural hybrids, mostly sterile. Some of these are discussed later. A study of these revealed some of the evolutionary patterns. The violets have utilized the methods of polyploidy in their processes of speciation. It was therefore no accident that the first example of polyploidy within a genus ($n = 6, 12, 18, 24, 36$) was in an early paper on chromosome numbers in violets (Miyaji, 1913). Written in Japanese and generally unknown to the rest of the scientific community, it was later translated to German (Miyaji, 1927).

SECTION CHAMAEMELANIUM

Within western North America the *Chamaemelanium* violets contain several evolutionally ascending species complexes (Clausen, 1951). These species complexes (cenospecies) are here considered subsections and are listed as *Pedunculatae*, *Purpureae*, *Nuttallianae*, *Chrysanthae*, *Nudicaules*, *Canadenses*, and *Biflorae*, the latter a less closely knit taxon. Species belonging to such distinct subsections can occur together within one and the same habitat; in contrast, the taxa within a single subsection occupy geographically or ecologically separate regions. The taxa within the subsection are therefore either ecotypic subspecies of one species, or they are ecospecies within a species complex. Experimental

evidence to determine between these two possibilities is not available except through natural hybrids.

At a nontropical latitude it is unusual to find so many distinct species complexes existing within a geographic region, as in *Chamaemelum*. The section is probably old, and the complexity mirrors evolutionary histories within a region that during millions of years has been geologically unstable. Obviously, many links with the past have been lost, although some still exist. The bridges between complexes are provided by species of recent discovery.

CHANGES IN CLASSIFICATION. The classification used in this paper differs slightly from Baker's. One of the changes (Baker, 1953) is that *V. aurea* ssp. *aurea* and ssp. *mohavensis* are here considered to be subspecies of *V. purpurea*. This is in accord with Baker's earlier concept and avoids the unnatural arrangement whereby *V. aurea* occurs as an island within the geographical territory of *V. purpurea*.

In contrast, *V. linguifolia* is retained as a species instead of being considered a subspecies of *V. praemorsa*. The morphological characters are not highly distinct in this case, although both the leaves and flowers of the two are different. There is reason to believe that the hexaploid *V. linguifolia* does not occur in the states of the Pacific slope. Forms from these more westerly regions previously thought to be *V. linguifolia* have consistently proved to be octoploid and belong to *V. praemorsa* ssp. *oregona* and ssp. *major*.

Viola praemorsa ssp. *praemorsa*, $n = 18$, from the coastal prairies, and 24 paired *V. praemorsa* ssp. *major* and ssp. *oregona* are retained as one species in accordance with Baker's classification. However, I do not feel that there is justification for maintaining *V. praemorsa* ssp. *arida* because ssp. *major* itself comes from the same transmontane arid region.

Another uncertainty exists in *V. bakeri* ssp. *shastensis* Baker. This taxon was referred to *V. bakeri* because it was thought to be octoploid, $n = 24$. Baker (1960) cited several specimens he thought belonged to the new taxon. A closer study of the type specimen, *Baker 13045*, from Postpile Camp in the Yolla Bolly Mountains, Tehama Co., and of *Baker 13139* from Scott Mountain, Trinity Co., on which the chromosome number was determined, indicates that they belong to different species. The type specimen has an elongated taproot and broadly lanceolate leaves with entire ciliate margins, scattered shaggy leaf pubescence, and pubescent capsules, the latter two characters separating it from the octoploid *V. bakeri* but placing it with the diploid relict *V. tomentosa*. The plant from Scott Mountain has an abbreviated truncate rootstock and crenulate leaf margins, placing it with the octoploid *V. praemorsa* ssp. *oregona* (table 1). The taxonomic status of the rare taxon, *V. bakeri* ssp. *shastensis*, and its chromosome number are therefore unknown. Most likely the taxon represents a disjunct population of the rare *V. tomentosa*.

SUBSECTION PEDUNCULATAE. The most coastal and southern of the North American *Chamaemelum* species is *Viola pedunculata*, $n = 6$

(table 1). This is the johnny-jump-up or wild pansy of California, which is remarkably adjusted to the California Coast Range climate of a mild, humid winter followed by a dry summer. It is a geophyte, having a deep-seated digitate roostock or bulb. During the winter and spring multitudes of underground stolons develop from the bulb, terminating into patches of flowering stems (Baker, 1949d). The stems dry up at the onset of summer, the plant becoming summer-dormant. This species occupies primarily the Coast Range regions of the southern half of California, including some offshore islands, and the northern part of Baja California. *Viola pedunculata* ssp. *tenuifolia* (table 1) occurs in scattered colonies in the inner Coast Ranges and the foothills of the Sierra Nevada.

Viola charlestonensis (Baker, 1949c) is a narrow endemic, high altitude counterpart limited to the Charleston Mountains of southeast Nevada. It is also diploid (table 1) and resembles *V. pedunculata* in the rounded outline of the leaves, its deeply buried roostock and its large seeds.

The scattered populations of the *Pedunculatae* suggest that this type of a violet previously had a wider distribution. Possible Mexican relatives are *V. flagcliformis* Hemsley and *V. galenaensis* Baker (Baker, 1947), the latter at 9000–12000 ft in the state of Nuevo Leon.

SUBSECTION PURPUREAE, AN EXAMPLE OF ECOLOGIC-GENETIC SPECIATION. *Viola purpurea* and its close relatives occupy most of the area from the Pacific to the Rocky Mountains, attaining an altitude of 11000 ft, but do not enter the prairie states. *Viola quercetorum* is cohabitant with *V. pedunculata* but is separated from it through its higher number of chromosomes, $n = 12$.

Leaf shapes of the various taxa within the *Purpureae* are pictured in Baker (1949d). Gross silhouettes of herbarium specimens of the succession of taxa are on a profile of western North America in Clausen (1951). West of the summits of the Sierra Nevada and the Cascades the taxa of this subsection have well developed aerial stems from root crowns in the surface of the ground; east of the summits the stem nodes are abbreviated, and the taxa native to the dry desert areas are geophytes having their renewal buds buried below the ground level.

One diploid species, *V. purpurea*, $n = 6$, extends from the 3000 ft level on the west side of the Sierra Nevada eastward to the Rocky Mountains and has developed about 10 distinct subspecies which replace each other through a series of climatic zones and edaphically distinct habitats.

1. *Viola purpurea* ssp. *purpurea* occupies the transition zone of California from about 3000–6000 ft, being associated with *Pinus ponderosa*, *Libocedrus decurrens*, and *Quercus kelloggii*. It is also associated with these species in the high mountains of southern California and in the northern California Coast Ranges (table 1). It has a tap root, rounded basal leaves with a truncate base, and aerial stems 10–15 cm long developing from the ground level. The type was collected by Kellogg near the

present day Placerville but was presumably destroyed in the San Francisco fire of 1906.

2. In the Sierra Nevada the change from ssp. *purpurea* to ssp. *mesophyta* coincides more or less with the replacement of *Pinus ponderosa* by *P. jeffreyi* and of *Quercus kelloggii* by *Q. vaccinifolia*. *Viola purpurea* ssp. *mesophyta* continues, however, throughout the territory of *Pinus murrayana*, following it to the summit of the passes at 10000 ft (table 1). It differs from ssp. *purpurea* by having shorter, more slender stems and distinctly narrower deltoid pubescent leaves.

3. The former two subspecies have finely serrate leaf margins, but north of the Lake Tahoe region and still on the west side of the mountains ssp. *mesophyta* is gradually replaced by ssp. *integifolia*, which differs from *mesophyta* primarily by having nearly entire leaf margins (table 1).

4. *Viola purpurea* ssp. *xerophyta* occupies gravelly terraces on the east side of the Sierra Nevada at or above 10000 ft (table 1). These tiny plants have stems buried in the gravel, renewal buds below the surface, and narrow, highly pubescent leaves. This subspecies is clearly related to the neighboring ssp. *mesophyta* and transitions are common near the passes. *Viola purpurea* ssp. *xerophyta* extends southward from the Lake Tahoe region to the San Bernardino Mountains of southern California.

5. *Viola purpurea* ssp. *geophyta* (table 1) is common in volcanic ash deposits at 4000–6000 ft east of the Cascades of central Oregon to Lassen Co., California, reappearing in the volcanic ash deposits of Mono Co. east of the Sierra Nevada. Its stems are deeply buried in ash and sand, the leaves are gray-pubescent and sinuate-toothed.

6. An interesting transitional ssp. *dimorpha* occupies a triangle in the northeastern corner of California (table 1) between ssp. *integifolia* and ssp. *geophyta*. Its spring leaves are mesic, resembling the leaves of the Great Basin ssp. *atriplicifolia*, but unlike other subspecies from east of the Cascades and Sierras ssp. *dimorpha* develops aerial stems in the summer.

7. The canescent *V. purpurea* ssp. *aurea* inhabits even drier zones than those inhabited by ssp. *geophyta*. It occurs locally east of the central Sierra Nevada in Washoe to Ormsby counties, Nevada, at about 4000 ft (table 1). Its stems and renewal buds are deeply buried in dry gravel.

8. *Viola purpurea* ssp. *mohavensis* (table 1) is morphologically related to ssp. *aurea*. Its herbage is gray, varying from smooth to short-pubescent, and like *aurea* its leaves are sinuate-toothed. It occupies dry sites in the higher parts of the Mohave desert and montane areas in southern California, 4000–7000 ft altitude. The lower parts of its stems are buried, but it develops about 10 cm long aerial stems.

Two subspecies occupy montane to alpine altitudes on the ridges of the Great Basin. Both are dwarfish and have green herbage, varying from smooth to slightly pubescent. Their renewal buds appear at the surface of

the ground and aerial stems are either absent or very short. They are:

9. *Viola purpurea* ssp. *atriplicifolia* has leaves of rounded outline with deeply sinuate leaf margins. It occurs from 6000–10000 ft altitude at widely scattered localities from eastern Washington, Oregon and California to Idaho and Wyoming.

10. *Viola purpurea* ssp. *venosa* is a dwarf alpine with subcordate and subentire leaves growing from eastern Washington, Oregon, and western Nevada to Montana, Utah, and Colorado.

Field and herbarium studies indicate that moderate recombinations of characters occur at the points where these taxa meet, suggesting some gene interchange. Such observations provide evidence that these taxa are subspecies adjusted to life in their particular environments rather than distinct species. Nevertheless, even though local crossings happen, the trends in subspecific replacements are fairly sharp, and the extremes are highly distinct. It is reassuring to notice how the characteristic leaf shape of ssp. *atriplicifolia* has been faithfully transmitted between points as remote as Yellowstone Park (type locality) and valleys on the east side of the Sierra Nevada.

An interesting example of the contiguous existence of the subspecies of *V. purpurea* from diverse areas is the Slate Creek Valley in the Harvey Monroe Hall Natural Area surrounding the Timberline transplant station of the Carnegie Institution of Washington. Within this east-facing hanging valley at 10000–11000 ft altitude, ssp. *mesophyta* occupies south slopes in the *Pinus murrayana* forest, ssp. *xerophyta* gravelly east-facing terraces at 10400 ft on Mount Conness, and the morphologically highly distinct ssp. *atriplicifolia* was found in grassy areas in the bottom of the valley at about 10000 ft. The three subspecies have therefore preserved their morphologic and ecologic identities over great distances.

Two tetraploid species, $n = 12$, are included in the *Purpureae* complex. Both of the tetraploids occupy environmental regions outside of the regions inhabited by the subspecies of the diploid *V. purpurea*. Geographically, therefore, these tetraploids are arranged as true members of the subsection *Purpureae*. Both tetraploids probably are amphiploids that combine diploid taxa belonging to separate subsections. The reasons for this assumption are to be discussed later in the paper.

Viola quercetorum, $n = 12$ (table 1) is a species of the oak savannas of the California Coast Ranges and the Sierra Nevada foothills, extending into the southern Oregon Coast Ranges (Baker, 1949a). In many characters it resembles the diploid *V. purpurea* ssp. *purpurea* of the Sierra Nevada transition zone and ssp. *mohavensis* of the arid transition zone at montane altitudes in southern California. In other respects, such as its semi-woody, much-branched rootstock, its long-pedicelled subcordate leaves, long-peduncled large flowers and generally large size, *V. quercetorum* reminds of the equally diploid *V. pedunculata* with which it is often cohabitant. *Viola quercetorum* follows *Quercus douglasii* and *Pinus sabiniana*, but above the 3000 ft level where these trees are being re-

placed by *Quercus kelloggii* and *Pinus ponderosa*, *V. quercetorum* is also replaced by the diploid *V. purpurea* ssp. *purpurea*.

Viola utahensis, $n = 12$ (table 1), is the other tetraploid of the *Purpureae*. It is a fairly narrowly endemic species in moister sagebrush lands of central Utah (Baker, 1949b). Occasionally *V. utahensis* is found together with the putative parents. The Utah violet combines subsections *Purpureae* with *Nuttallianae*, whereas *V. quercetorum* possibly is a *Purpureae-Pedunculatae* combination.

**SUBSECTION NUTTALLIANAE, DIFFERENTIATED THROUGH POLY-
PLOIDY.** In contrast with the *Purpureae* the *Nuttallianae* constitute a polyploid species complex. The chromosome number of its species range from $n = 6$ to 24 at intervals of six pairs of chromosomes. The species of the *Nuttallianae* cover western North America from the coastal plains of the Pacific in Washington to the western prairie states east of the Rocky Mountains, although they are absent in the Coast Range regions from central California southward.

With one exception, the species of the *Nuttallianae* differ from the *Purpureae* by having glabrous seed capsules compared with appressed puberulent capsules in the *Purpureae*. The *Nuttallianae* generally lack elongated aerial stems, and their basal leaves (Baker, 1957; Clausen, 1951) are much larger and of a different shape than those of the *Purpureae*. Since the members of the two subsections mostly cover the same area they often cohabit.

The *Nuttallianae* subsection has two basic diploid species, each with its morphologically distinct series of polyploid derivatives. The diploids are geographically separated: one, in the central Sierra Nevada has taproot and entire leaves with ciliate margins, and the other, in the intermountain region, has abbreviated, truncate rootstock and crenulate, non-ciliate leaf margins.

1. *Viola tomentosa*, $n = 6$ (table 1), is the Sierra Nevada diploid, a recently discovered rare endemic at 5000–6000 ft from Eldorado to Plumas counties (Baker, 1949b). It is a highly distinctive violet with a taproot similar to that of *V. purpurea* and small, lanceolate leaves (Baker, 1949d). It differs from others of the *Nuttallianae* by having densely tomentose leaves, woolly pubescent capsules and fairly well developed stems in the fruiting stage (Baker, 1957). It combines, therefore, characters of the *Nuttallianae* with those of the *Purpureae* and hybridizes with the equally diploid cohabitant *V. purpurea*, although the hybrids are sterile (see later).

2. *Viola bakeri*, $n = 24$ (table 1), is the only polyploid species that is morphologically and geographically related to the diploid *V. tomentosa*. Before its chromosome number was known, *V. tomentosa* was even suspected of being a subspecies of *V. bakeri*. The octoploid *V. bakeri* has a long taproot and lanceolate leaves with entire, ciliate margins, but it has glabrate capsules and lacks the tomentose pubescence and the elongated summer stems that characterize *V. tomentosa* (Baker, 1957). *Viola*

bakeri is a montane species of forested areas, ranging at altitudes of 5000–6000 ft from southern Washington through the Cascade Mountains of Oregon to the central Sierra Nevada where it surrounds *V. tomentosa*.

No hexaploid species is known that with *V. tomentosa* could produce the octoploid *V. bakeri*, unless the extremely rare *V. bakeri* ssp. *shastensis* (Baker, 1960) should prove to be the missing hexaploid. Morphologically, however, ssp. *shastensis* classifies as a geographically well separated, less tomentose population of *V. tomentosa*. It could also be a relict hybrid derivative of *V. tomentosa* with *V. bakeri*.

3. *Viola vallicola*, $n = 6$ (table 1), is the inter-mountain diploid that presumably is one progenitor of a couple of polyploid derivations. It has a truncated vertical rootstock; thin, smooth ovate leaves with truncate base and crenulate, non-ciliate leaf margins (Baker, 1957). It is a species growing in grassy and open wooded areas in the mountains, among sagebrush with some moisture, and in grassy prairies. It has the widest distribution of any species within the *Nuttallianae*, ranging from eastern Washington, Oregon and Nevada to Alberta, the Black Hills of South Dakota, Wyoming and Colorado, altitudes 4500–7500 ft.

4. *Viola nuttallii*, $n = 12$, is the only tetraploid species among the *Nuttallianae*, a prairie species that remains east of the continental divide. It is a geophyte, having a deep seated truncated rootstock with the renewal buds below the surface, and lanceolate, puberulent leaves with crenulate margins. The morphology contradicts that *V. nuttallii* could be an autopoloid of *V. vallicola* as suggested by Baker (1957). Chromosomes have been counted only on plants from Canada and Colorado (table 1), and undiscovered diploid *V. nuttallii* could exist somewhere within the large area of the species, extending from Arizona, eastern Colorado, Wyoming, Montana to Alberta, North and South Dakota, Nebraska, and Kansas.

5. *Viola linguifolia*, $n = 18$ (table 1), is a montane to subalpine forest violet of the Great Basin Ranges, 2500–10000 ft altitudes. It is a hexaploid member of the *V. vallicola* derivatives, possessing the key characteristics of the group; short, erect, truncate rootstock and crenulate-margined, non-ciliate, erect elongated-ovate leaves; the floral peduncles do not surpass the leaves (Baker, 1957). The leaf shape suggests a compromise between the leaves of *V. vallicola* and *V. nuttallii*, but *V. linguifolia* is larger than either and occupies a moister, higher altitude zone than either. *Viola linguifolia* extends from eastern Washington, Oregon and western Nevada to Montana, Wyoming and Colorado.

6. Another closely related hexaploid of this group, *V. praemorsa* ssp. *praemorsa*, $n = 18$ (table 1), occupies the coastal prairies of Washington, Oregon, and northern California at low altitudes. It differs from *V. linguifolia* in having divaricate leaves with cordate bases, and the flowers on the equally divaricate peduncles surpass the leaves (Baker, 1957). It is densely pubescent with long hairs. Douglas's name, *V. praemorsa*,

refers to the truncated rootstock that is so characteristic of the polyploid violets derived from *V. vallicola* and *V. nuttallii*.

A gap of at least about 150 mi separates the coastal *V. praemorsa* from the nearest recorded interior and essentially montane *V. linguifolia*; this gap is now occupied by the Cascade Mountains. It is tempting to suggest that before the rise of the mountains these two hexaploids were connected across the then low plains.

The mountains and valleys of the Pacific states that now lie between the coastal prairies and the inter-mountain region provide habitats for three octoploid *Nuttallianae* taxa, $n = 24$, that probably are conglomerates of several origins. One of these, the tap-rooted *V. bakeri*, $n = 24$, was discussed in connection with the Sierra Nevada diploid, *V. tomentosa*, $n = 6$. Two other octoploids, relating to the inter-mountain *V. vallicola* diploid and to the hexaploids on both sides of the Cascades-Sierra Nevada, have the *praemorsa* type truncated rootstock and the crenulate, non-ciliate leaf margins and will be discussed below.

7. *Viola praemorsa* ssp. *major*, $n = 24$ (table 1), is the largest and most robust of the taxa within the *Nuttallianae*. It differs from ssp. *praemorsa* by its leaves equaling or surpassing the flowers, by generally erect leaves and peduncles and larger flowers (Baker, 1957). These characters are fairly well correlated with the chromosome number and particularly with the geographic distribution. This taxon was first described by Hooker as a variety of *V. nuttallii* on the basis of Douglas' specimens taken "under solitary pines on the dry, sandy soil of the Columbia," presumably somewhere near the present Hood River, Bingen, and the Dalles.

Viola praemorsa ssp. *major* occurs from Washington and central California in a broad band through the Cascades and the Sierra Nevada with extensions to neighboring mountains and intervening valleys at altitudes from about 600–6000 ft. The border between *V. praemorsa* ssp. *major* and *V. linguifolia* follows closely the dividing line between Washington-Oregon (in ssp. *major* territory) and Idaho (in *V. linguifolia* territory). There is a westward bulge of ssp. *major* into the northern California Coast Ranges and the Siskiyou Mountains of California and Oregon, where it meets ssp. *praemorsa*.

8. *Viola praemorsa* ssp. *oregona*, $n = 24$, has broadly lanceolate basal leaves, resembling *V. linguifolia*. It occupies a small area at mid-altitude in southeastern Oregon and northeastern California (Baker, 1957).

The taxonomist has good reason to become confused by the octoploid "muddle" of *V. praemorsa* ssp. *major*, ssp. *oregona*, and *V. bakeri* from the same general territory. These taxa are less distinct than the diploids, and it appears that an octoploid complex species is in the process of emerging through genetic interchange between the elements. The individuals within each population are highly variable, and the populations differ from each other. Such differences go unnoticed until the herbarium sheets from each local population have been gathered from the various herbaria throughout the country.

From an over-all point of view it appears that *V. praemorsa* ssp. *major* is morphologically related to hexaploid ssp. *praemorsa* on the coast, whereas ssp. *oregona* is suggestive of the hexaploid *V. linguifolia* to the east, but no present-day diploids are known that with the hexaploids could synthesize the octoploid subspecies. Hexaploid and tetraploid progenitors of *V. bakeri* are also missing. The present chromosome survey is very limited, providing only a skeleton to which substance can be added.

SUBSECTION CHRYSANTHAE. The yellow-flowered violets of the *Chrysanthae* have rosettes of deeply dissected leaves, deep seated rootstocks, and long-peduncled flowers on short aerial stems. They constitute a strictly polyploid complex through the states of the Pacific slope. With the species of both *Purpureae* and the *Nuttallianae* they produce sterile, natural hybrids.

Viola sheltonii, $n = 6$ (table 1), is the only known diploid species within this subsection. It has palmatisect leaves of cordate outline and hybridizes with *V. tomentosa* of the *Nuttallianae*.

Viola beckwithii T. & G. and *V. trinervata* Howell have leaves of similar outline to those of *V. sheltonii*, although they are palmatifid rather than palmatisect. They are native to the northern Great Basin, but their chromosome numbers are not known.

Viola douglasii and *V. hallii* have bipinnatifid leaves of ovate outline. *Viola douglasii* is native to the inner Coast Ranges and foothills of the Sierra Nevada from Kern Co. to Oregon. It is tetraploid, $n = 12$, in its southern half, and octoploid, $n = 24$, north of the San Francisco Bay (table 1). It hybridizes with species of the *Purpureae* and the *Nuttallianae*.

Viola hallii, $n = 36$ (table 1; Gershoy, 1932) is a 12-ploid species of the northern Coast Ranges.

The chromosome numbers of $n = 18$ and $n = 30$ are still missing in completing the polyploid series within this subsection, but the two Great Basin species above might provide them.

SUBSECTION NUDICAULES. This subsection has erect succulent stems, usually poorly developed rosette leaves, and yellow flowers. The *Nudicaules* extend to eastern North America and to east Asia and are inhabitants of fairly humid woods and forests. The diploid *V. lobata*, $n = 6$, and the only tetraploid, *V. glabella*, $n = 12$, are western species. A diploid close relative of the latter is the Japanese *V. brevistipulata*, $n = 6$ (*V. glabella* in Miyaji, 1913). Other diploid relatives grow in eastern North America and in Japan (table 1).

SUBSECTION CANADENSES. This subsection constitutes a complex of species that also have prominent and erect but leafy stems but have whitish to purple, rather than yellow flowers. The *Canadenses* have species both in western and eastern North America, including two diploid species, *V. ocellata*, and *V. scopulorum*, $n = 6$, and two tetraploids *V. canadensis*, and *V. rugulosa*, $n = 12$ (table 1). Bold and Gershoy (1934)

found that the latter two intercrossed easily and their hybrids appeared fully fertile. The chromosome numbers of two western species of this complex *V. cuneata* and *V. flettii* are not known.

SUBSECTION BIFLORAE. In a previous paper Clausen (1929) stated that it would be logical to consider the yellow-flowered *V. biflora*, $n = 6$, a *Chamaemelianium* violet. In certain respects this species is among the least differentiated species of the section and of the genus as well. In 1929 the term *Biflorae* was applied only to *V. biflora* and *V. sarmentosa* (synonym: *V. sempervirens*).

A better understanding of the *Biflorae* is now possible. They constitute a loosely knit group of species that previously were scattered among the sections *Dischidium*, *Chamaemelianium*, and *Plagiostigma*. The *Viola* sections were based exclusively on the characters of the pistil and stigma. These make sensible distinctions between such sections as *Melanium*, *Plagiostigma*, and especially *Rostellatae* (Clausen, 1929) that were best known to European botanists. In contrast, within the *Chamaemelianium* section the species-to-species variability in pistil-stigma characters is greater than the section-to-section variability of the other violets (Clausen, 1929).

As here interpreted, the *Biflorae* follow the distinctive chromosomal pattern of the *Chamaemelianium* violets, have yellow flowers, and a central corm from which emerge either the flower-bearing but weaker horizontal stolons or rhizomes, or short ascending runners. The *Biflorae* are inhabitants of humid woods, forests and mountains.

The best known western species of the *Biflorae* is *Viola sempervirens*. Within the redwood forests of central California it is a tetraploid, $n = 12$ (Clausen, 1929), but it is octoploid, $n = 24$, at lower altitudes in the forests of Oregon (Gershoy, 1934). The closely related *V. orbiculata*, $n = 12$ (Gershoy, 1932), is a species of higher altitudes in humid mountain forests of the northern Cascades and beyond; it has ascending, short runners.

Another member of the *Biflorae* is *V. rotundifolia*, $n = 6$ (Gershoy, 1928). This is a yellow-flowered violet of cool, rich woods in eastern North America. It was previously classified with the section *Plagiostigma* on account of the shape of its pistil and stigma (Clausen, 1929), disregarding its flower color and chromosome number. *Viola rotundifolia* is reminiscent of the tetraploid western *V. orbiculata* by its gross morphology and by its short, rambling summer stems (Baird, 1942).

The name-giving species of the complex is *V. biflora*, $n = 6$ (table 1). Because of its primitive pistil and split stigma it was previously referred to the monotypic section *Dischidium*, but this character is also found in other genera of the family. The pistil of *V. sempervirens* represents a transition from that of *V. biflora* (Clausen, 1929). *Viola biflora* has a short, thick rootstock from which rambling, deciduous flowering stems emerge; these contrast with the evergreen, trailing, flower-bearing stems of *V. sempervirens* from a more southern latitude.

Viola biflora is a montane and high latitude circumpolar species that reaches western North America in Alaska and also occurs in isolated locations within the Pikes Peak region of Colorado. Gershoy (1934) produced a weak hybrid between *V. biflora*, $n = 6$, and *V. rugulosa*, $n = 12$, an indication that a degree of genetic relationship exists between *V. biflora* and a *Chamaemelanium* violet.

In Japan (table 1) the diploid *V. biflora* remains below 1500 m altitude. Above 2100 m it is replaced by a closely related octoploid, *V. crassa*, $n = 24$ (Miyaji, 1929).

Chromosomally and otherwise *V. biflora* appears to belong to a primitive group within the *Chamaemelanium* section, a group that has highly divergent pistil and stigma characters. Such a situation suggests that the *Biflorae* are central among the violets of the northern hemisphere and therefore are related to several sections of the genus *Viola* and probably to other genera as well.

NATURAL INTER-SUBSECTIONAL HYBRIDS OF CHAMAEMELANIUM. 1. *Purpureae* \times *Nuttallianae*; *V. purpurea*, $n = 6$, \times *V. tomentosa*, $n = 6$. Two hybrid localities were discovered by Baker within the territory of *V. tomentosa*. One was in Nevada Co. near Excelsior Point at 5000 ft in the yellow pine and incense cedar zone (*Baker 8729*) where the parental *V. purpurea* ssp. *purpurea* and *V. tomentosa* were found nearby. The other was at Little Grass Valley, Plumas Co. (*Baker 9968*), also there between parents, but in this case the *purpurea* parent belonged to ssp. *integrifolia* (*Baker 9970*) and the *V. tomentosa* parent was *Baker 9969*. In leaf form the hybrids resemble the *V. purpurea* parents but they possess shaggy, scattered pubescence reminding of the *V. tomentosa* parents. Both hybrids were fixed for chromosome investigations but were too old for meiosis. The pollen size varied greatly in both, suggesting unequal distribution of the parental chromosomes and accordingly general lack of homology. The seed capsules contained empty seeds. Obviously, *V. purpurea* and *V. tomentosa* are only remotely related, although the existence of the normally developing hybrids indicates a measure of genetic relationship between the parental species.

2. *Chrysanthae* \times *Purpureae*; *V. douglasii*, $n = 12$, \times *V. quercetorum*, $n = 12$. Throughout its tetraploid area *V. douglasii* regularly crosses with the equally tetraploid *V. quercetorum*, whenever they occur in the same habitat. Hybrids have been found in both Kern Co. and Santa Clara Co. and are completely sterile. In growth form the hybrids resemble the *V. douglasii* parent: they are geophytes, having their renewal buds buried below the ground surface. The hybrids are easy to recognize, however, as their leaves are pinnatifid instead of pinnatisect. Hybrids of this kind were found in the foothills west of Glenville, Kern Co. (*Keck & Clausen, 3188*), and in the village of Glenville (*Keck & Clausen, 3194*). In Santa Clara Co. on the east side of the Mount Hamilton Range at Arroyo Bayo, similarly growing with *Quercus douglasii* and *Pinus sabiniana*, another hybrid population was discovered between the

parental species (*Keck & Clausen, 4546*). In the Kern Co. hybrids the 24 chromosomes were arranged in six pairs plus 12 single chromosomes, but the meiosis was more irregular in the Santa Clara Co. hybrid (table 1). It is not known whether the six pairs derive from conjugation between *douglasii* and *quercetorum* chromosomes or from autosyndesis among the chromosomes of one of the parent species.

A hybrid *V. douglasii* \times *V. purpurea* was reported by Baird (1936). This was before *V. quercetorum* was published. The hybrid was collected with the parent species on April 18, 1935, in Walker Basin, between Caliente and Bodfish, Kern Co., on sunny slopes. The altitude of the Basin is approximately 3500 ft, and Mrs. Baird agreed that the altitude she quoted, 6000 ft, was too high. The Keck and Clausen hybrids were collected on April 13 the same year around Woody and Kernville, only about 30 mi farther north. Mrs. Baird's careful description suggests that her *V. purpurea* was the tetraploid *V. quercetorum*, although her drawing is somewhat suggestive of the diploid *V. purpurea* ssp. *mohavensis*. Lacking the chromosome numbers of the Baird specimens the parentage of this hybrid cannot be decided with certainty. No seed developed on the garden transplant of this hybrid.

Within the octoploid territory of *V. douglasii* a cytologically puzzling *V. douglasii* plant was found that could be a hybrid derivative of *V. douglasii* \times *V. quercetorum*. This plant (*Baker 8645*) from Indian Valley, Plumas Co., has 29 pairs and one single chromosome, $2n = 59$ (cited as *V. douglasii* in table 1). This plant occurred with *V. quercetorum*, $n = 12$ (*Baker 8644*, table 1). Baker suspected hybrids in this population and transplanted the *V. douglasii* plant to Kenwood, where the buds were fixed. It is possible that an unreduced *V. douglasii* ovule, $2n = 48$, pollinated by a reduced *V. quercetorum* pollen, $n = 12$, could result in a subdecaploid hybrid derivative, $2n = 59$. The *douglasii* chromosomes would be expected to pair among themselves, providing about 24 pairs and possibly 6 pairs of *quercetorum* chromosomes, equaling about 30 pairs. In such a hybrid the proportion of *douglasii* : *quercetorum* chromosomes would be 80 : 20 per cent, strongly in favor of *douglasii*. In comparison, the proportion is 50 : 50 per cent in the tetraploid hybrids (above), and in the octoploid hybrids discussed below. Morphologically, the 50 : 50 hybrids are already overwhelmingly towards *V. douglasii*. The strong hereditary influence of the species of the subsection *Chrysanthae* widens the possibilities concerning the ancestry of the species of that subsection.

3. *Chrysanthae* \times *Nuttallianae*: *V. douglasii*, $n = 24$, \times *V. praemorsa* ssp. *major*, $n = 24$. Applegate discovered this hybrid (*Applegate 8319*, DS) in a narrow zone between the parental species on an exposed rocky slope among junipers and sagebrush in 1933 (table 1). During the first meiotic metaphase of the hybrid 48 unpaired chromosomes were observed, suggesting general absence of homology between the parental chromosomes. The hybrid was completely sterile. Morphologically, this

octoploid Oregon hybrid is indistinguishable from the tetraploid California hybrids of *V. douglasii* \times *V. quercetorum*. Both kinds of hybrid have pinnatifid rather than pinnatisect leaves and would pass as belonging to the subsection *Chrysanthae*. In both kinds of hybrid the proportion of *douglasii* to other chromosomes is comparable. This fact, and the penetrating influence of *V. douglasii* makes the similarity understandable.

4. *V. sheltonii*, $n = 6$, \times *V. tomentosa*, $n = 6$. The hybrid (near Weaver Lake, Sierra Co., *Baker & Smith 8726*) between these two diploid species grew with *V. tomentosa* in open coniferous forests at 5400 ft altitude. It had somewhat tomentose pinnatifid leaves, suggesting its origin, but was not fixed for cytological investigation.

POSSIBLE NATURAL AMPHIPLOIDS. The *Chamaemelanium* section has evolved an unusual superstructure of polyploid species, ranging from diploid to 12-ploid. A survey of the arrangement of the species within the various polyploid levels was previously given (Clausen, 1951). Many amphiploids are expected in such a group, but the identification of the parents of natural amphiploids is generally hazardous.

The safest principle in identifying amphiploids is to use the geographic-ecologic distribution of the amphiploid and its putative parents supported by their gross morphological characters and chromosome numbers. The morphology of the inter-subsectional hybrids listed above suggests that *Viola* hybrids can be deceptive. In general, the parents of successful natural amphiploids are fairly remotely related and belong to distinct cenospecies, that is, in the *Chamaemelanium* section they may belong to distinct subsections.

1. *Viola quercetorum*, $n = 12$: Suggested parent species, *V. pedunculata*, $n = 6$, and *V. purpurea*, $n = 6$. Characters of *V. quercetorum* that remind of *V. pedunculata* are long peduncles, large petals, broadly subcordate lower leaves, branched rootstock, widely spreading habit, and especially its climatic region. Its morphological similarity to *V. purpurea* is obvious. *Viola quercetorum* occupies an ecological zone that became available after the rise of the Coast Ranges and after the development of the oak woodlands between the coast and the coniferous forests of the lower Sierra Nevada. Before that time *V. pedunculata* must have found congenial habitats over a considerably larger territory than now because the coastal influence reached much farther inland. Stebbins et al. (1963) claims that *V. purpurea* ssp. *mohavensis* and ssp. *purpurea* were the parents, and that *V. pedunculata* was not a parent. They base the conclusion upon chromatographic evidence but are aware that their two putative parents are natives of cold winter climates, whereas *V. quercetorum* occupies a climatically milder zone. Since *V. pedunculata* probably was contiguous to *V. purpurea* ssp. *purpurea* in Pliocene central California and to relatives of ssp. *mohavensis* in Pleistocene southern California it is possible that *V. quercetorum* may have arisen more than once, from crossings between *V. pedunculata* and the two subspecies of *V. purpurea*.

The high morphological variability within *V. quercetorum* and especially the difference between southern and central California plants of the species lend credence to this possibility.

I wholeheartedly agree with the plea by Stebbins et al. (1963) concerning the need for an extensive cytological investigation of the *V. purpurea* relatives, especially in southern California. I disagree, however, with the interpretation of the distribution of subspecies presented in the map, especially the exclusion of ssp. *purpurea* from southern California and the extension of *V. quercetorum* to an altitude of 7000 ft. The last three *V. quercetorum* plants listed (Stebbins et al., 1963; table 1) belong to *V. purpurea* ssp. *mohavensis* or are introgressive hybrids between ssp. *mohavensis* and ssp. *purpurea*.

2. *Viola utahensis*, $n = 12$: suggested parent species, *V. vallicola*, $n = 6$, and *V. purpurea* ssp. *venosa*, $n = 6$. The narrowly endemic sagebrush species, *V. utahensis* (Baker, 1949b), is ecologically and morphologically intermediate between *V. vallicola* at 4000–6000 ft in open sagebrush flats, and *V. purpurea* ssp. *venosa* of moister, forested habitats, 5000–10000 ft, combining diploid species of subsect. *Nuttallianae* and *Purpureae*. Its herbage and seed capsules are minutely puberulent as in *Purpureae*. The amphiploid can occasionally be found together with both putative parent species and is probably of recent origin.

3. *Viola linguifolia*, $n = 18$: suggested parent species *V. vallicola*, $n = 6$, and *V. nuttallii*, $n = 12$. *Viola linguifolia* has broadly lanceolate leaves with ovate base, *V. vallicola* ovate leaves with truncate base, and *V. nuttallii* lanceolate leaves, tapering at both ends. *V. nuttallii* is distinctly a prairie species, *V. vallicola* a species of sagebrush flats and open woods in the intermountain region, extending to the prairie region, whereas *V. linguifolia* is a species of montane regions, 5000–8000 ft. The two putative parents occasionally occur together, as for instance near Hulett, Crook Co., NE Wyoming at 4500 ft, where *Ownbey 543–544* is *V. nuttallii* from loose soil and steep hillsides, and *Ownbey 553* is *V. vallicola* from grassy parks and divides.

SECTION MELANIUM

The homogeneity in the series of chromosome numbers of the *Chamaemelanium* section contrasts with the irregularity in the *Melanium* section, or the field pansies (Clausen, 1931). One group of its species appears to follow a modified 6-series, $n = 7, 8, 11, 12, 13, 17, 18$, and 24, and a different group a 10-series, $n = 10, 20$, and 30. Both in chromosome numbers and in their pistil character the 6-series pansies resemble certain species of *Chamaemelanium*, such as *V. pedunculata*.

The *Melanium* violets are almost exclusively European and west Asiatic, but one species, *V. rafinesquii*, Greene, $n = 17$, is a native North American species. It is a weedy annual predominantly of the southeastern states but reaches western North America in Colorado. The history

and relationships of this species are discussed in a separate paper (Clausen, Channell, and Nur, 1964).

SECTION PLAGIOSTIGMA

Most of the species of the *Plagiostigma* section have chromosome numbers in multiples of 12 rather than in multiples of 6, but two of its groups deviate by having aneuploid numbers. Chromosomally the *Plagiostigma* violets could be considered to have been derived from an original 6-series. None have yellow petals. Examples of pistils and stigmas were shown in Clausen (1929).

SUBSECTION STOLONOSAE (PALUSTRES). The relatives of *V. palustris* are a circumpolar group of species of moist meadow habitats or even shallow bogs. The tops of their pistils are flattened or even expanded and provide a platform with a conical stigmatic papilla along the margin of the platform, a shape also found in some members of the *Chamaemelum* section. The flowers are white or lavender.

The *Stolonosae* of North America comprise many diploids, $n = 12$ (table 1), and include *V. mccabeiana*, a local British Columbia species which Baker (1940) and Baird (1942) related to *V. nephrophylla*, $n = 27$, of the *Boreali-Americanae*. Its chromosome number, slender rhizomes, and ecology places it now with the *Stolonosae*. One species, *V. epipsila*, $n = 6$, is circumboreal, but the chromosome number of its western ssp. *repens* is unknown. A belt of delicate mountain bog species comprises *V. macloskeyi* (west coast and mountains) and *V. pallens* (eastern counterpart) and possibly even *V. mccabeiana*. Another belt of coarser plants at lower altitudes is *V. occidentalis* (western), *V. lanceolata* (eastern), *V. vittata* (southeastern), and *V. primulifolia* (eastern half of continent). Gershoy (1932) recorded fertile F_1 hybrids of *V. pallens* pollinated by *V. lanceolata* and *V. primulifolia*, suggesting close genetic relationships between species of both belts.

Viola palustris, $n = 24$ (Gershoy, 1928) is a tetraploid, circumpolar species. In the wild it hybridizes with other members of the complex (Clausen, 1927). The western North American *V. palustris* ssp. *brevipes*, appears to be such a polyploid, chromosomally irregular hybrid derivative (table 1). Since only a couple of samples of the *V. palustris* complex have been chromosomally investigated, it can be expected that a more extensive study will provide more surprises.

SUBSECTION VAGINATAE (LANGSDORFFIANAE). This is a small essentially east Asiatic to western North American group of species. Three diploid species, $n = 12$, are known from Japan in addition to the octoploid *V. langsdorffii* (Regel) Fisch., $n = 48$ (Miyaji, 1929). *Viola langsdorffii* also occurs in the Aleutian Islands and in Alaska, but its chromosome number within that region is not known. Neither is the number known of the closely related *V. simulata* Baker of moist woody areas of the Pacific coast from British Columbia to Oregon.

SUBSECTION ADNATAE. The *Adnatae*, exemplified by *V. patrini* DC., $n = 12$, are distinguished by having the stipules attached to the pedicels. They constitute a huge east Asiatic polyploid complex of at least 24 species, having chromosome numbers of $n = 12, 24, 36$ (listed as *Plagiostigma* and *Umbrosae* by Miyaji, 1929). Scattered members of the *Adnatae* occur beyond east Asia and include the western North American and circumpolar diploid *V. selkirkii* Pursh, $n = 12$ (Gershoy, 1928, Miyaji, 1929) of the cool mountain forests and the European tetraploid *V. pinnata* L., $n = 24$, of the Swiss Alps (Clausen, 1927).

SUBSECTION BLANDAE. The *Blandae* are chromosomally separated from other species of the *Plagiostigma* section in having a subtetraploid number of chromosomes, $n = 22$ (table 1; Gershoy, 1932). They consist of a species pair, *V. blanda* and *V. incognita*, eastern species that reach as far west as Minnesota and the Dakotas.

SUBSECTION BOREALI-AMERICANAE. The North American stemless blue violets constitute another aneuploid group of the *Plagiostigma* section, consisting of approximately 30 species such as *V. cucullata* Ait. and *V. palmata* L. All are hypertetraploids, having $n = 27$ (Gershoy, 1928). They have pistils and stigmas similar to those of the *Stolonosae* but can be distinguished from them by their heavy, succulent rootstocks or rhizomes. Predominantly the *Boreali-Americanae* are an eastern North American group of taxonomically closely knit species that were made famous by Ezra Brainerd's classical studies on Mendelism in wild violets during the early years of this century (Brainerd, 1906; 1921; 1924).

Following Brainerd's field and garden studies Gershoy (1928; 1932; 1934) determined the chromosome numbers of the *Boreali-Americanae* and found them generally fairly interfertile. The aneuploid chromosome number of the group tends to separate them genetically from the other *Plagiostigma* violets. Before white man came to North America the taxa of the *Boreali-Americanae* occupied edaphically distinct niches within the huge forests of the continent. Their genetic barriers were only partial, however, and when new avenues for migration were opened through clearings in the forests they expanded their territories, hybridized, and entered an evolutionary cycle of adjustment to man-made environments.

Viola nephrophylla is the only species of the *Boreali-Americanae* that extends all the way from the Atlantic coast across the continent to the Pacific states. It and two close relatives, *V. cognata* and *V. arizonica* Greene, are the only western North American representatives of the group, the latter two by some authors considered varieties of the former. Chromosomally, a western form of *V. nephrophylla* and *V. cognata* are similar to the eastern taxa of the complex, having $n = 27$ chromosomes (table 1).

Viola clauseniana conforms in gross morphology with the *Boreali-Americanae*, but it differs by having smooth, beardless petals and by a rare chromosome number $n = 22$ (table 1), one similar to that of the *Blandae*. According to Baker (1938) *V. clauseniana* occupies a precari-

ously small, specialized habitat, not more than about 100 ft in diameter in Zion National Park, Utah, growing in a canyon at the base of Weeping Rock, a spot where sunlight seldom, if ever, comes. *Viola nephrophylla* lives in the same general region, and *V. arizonica* was found at a higher altitude of 9000 ft. *Viola clauseniana* exemplifies how among the violets a species can become genetically isolated from most of its morphologically closest relatives.

Another violet that in gross morphology is loosely reminiscent of the *Boreali-Americanae* is *V. pedata* L., $n = 28$ (Gershoy, 1932). It has, however, a very different pistil, and genetically it is a highly isolated species. In crossings with species of the *Boreali-Americanae*, *Adnatae*, *Canadenses*, *Rostellatae*, and others Gershoy (1932) obtained no seeds or only seeds unable to germinate.

SECTION ROSTELLATAE

The stemmed blue violets of North America belong to one of the groups of the section *Rostellatae*. These are circumboreal and have chromosome numbers in multiples of 10, rather than of 6 or 12 as in the previous sections. In the *Rostellatae* the pistil ends in a straight or curved beak or rostellum, and the stigma is at the end of the beak (Clausen, 1929). Most of the species of the *Rostellatae* are Eurasiatic, but one of its subsections is circumboreal and has representatives in western North America. The three subsections of the *Rostellatae* (Clausen, 1931b) are: 1. *Arosulatae* Borb., Eurasiatic; simple biaxial growth habit as in the *Nudicaules* and in *Canadenses* of the section *Chamaemelum*, the primary stems elongate, and the flowers emerge from the leaf axils; $n = 10$ in *V. stagnina* Kit., $n = 20$, in *V. elatior* Fries and *V. canina* L. (Clausen, 1926; 1927; 1929); some populations of the latter have accessory chromosomes (Clausen, 1931a); the Atlantic coastal *V. lactea* Sm. is subhexaploid and has $n = 29$ (Moore, 1959); 2. *Scapigerae* W. Beckr., Mediterranean-West Asiatic; biaxial, but nodes of primary stems do not elongate, and flowers develop from the axils of the rosette as in *V. semper-virens* and in *Boreali-Americanae*; $n = 10$ in *V. odorata* L. and *V. hirta* L.; $n = 20$ in *V. sepincola* Jord; 3. *Rosulantes* Borb., Eurasiatic and North American; triaxial, the primary stem develops a leaf rosette only and flowers appear from elongated secondary stems that come from the axils of the rosette as in the western North American *V. adunca*; $n = 10$ in *V. rupestris* Schmidt and *V. reichenbachiana* Jord., $n = 20$ in *V. riviniana* Reich., some populations of the latter having accessory chromosomes (Valentine, 1949).

SUBSECTION ROSULANTES. *Viola adunca*, $n = 10$, occupies habitats from the Pacific coast to altitudes of 10000 to 12000 ft in the high Sierra Nevada and beyond to the intermountain region and the Rocky Mountains (Clausen, Keck, and Hiesey, 1940). No exception to $n = 10$ has been found (table 1). The inland and higher altitude forms differ in

morphology from the type of the species which came from the Northwest coast. Many segregate names have been proposed for these taxa. Since the changes with altitude parallel those of the subspecies and ecotypes of *Potentilla glandulosa* from the same general region, and since the chromosome numbers in about 55 taxa and natural hybrids of western North to be one huge species with many subspecies (table 1).

Viola howellii is a tetraploid and octoploid counterpart of *V. adunca* (table 1). It occurs in the lower Coast Ranges, valleys, and lower Cascade Mountains of Oregon and Washington. Gershoy (1928) found that plants sent by Peck of Willamette University were tetraploid (probably $n = 20$). In contrast, plants from near the type locality of the species, at Oregon City near Portland, Oregon, were octoploid, $n = \text{ca. } 40$ (Gershoy, 1932). From this preliminary sampling it is obvious that *V. howellii* merits a more thorough chromosomal study throughout its territory.

The stemmed blue violets of eastern North America are chromosomally uniform: Gershoy (1928; 1932) reported $n = 10$ in *V. conspersa* Reichb., *V. labradorica* Schwein., *V. rostrata* Pursh. and *V. striata* Ait. Miyaji (1913; 1929) likewise found $n = 10$ in 10 Japanese species of *Rostellatae*. The existence of 10 as a basic number in the *Rostellatae* from three continents is therefore well established.

Attention is called to the fact that the pistils of the two western members of the *Rostellatae* tend to expand into a head (Clausen, 1929), approaching in this character some of the western *Chamaemelanium* species and deviating from *Rostellatae* in other parts of the world.

CONCLUSIONS

This paper documents approximately 115 determinations of chromosome numbers in about 55 taxa and natural hybrids of western North American violets (table 1). The text discusses the taxonomic, ecologic, geographic, and evolutionary aspects of the chromosome situation of these taxa and of their relatives in other parts of the world.

The *Viola* genus probably has some 600 species distributed among about 14 sections in northern and southern hemispheres. The sections of *Viola* are more like genera among other plants, but it would be taxonomically unwise to partition the genus *Viola*. It has evolved a unique and distinctive floral apparatus that makes it easy to recognize a violet in any part of the world. Four sections are native to the temperate zones of the northern half of our earth, and all four are represented within our area.

The *Chamaemelanium* section is evolutionally distinct from the other sections of the genus by strictly following a polyploid series of chromosome numbers with $x = 6$ as the basic number. All levels of polyploidy from the diploid $n = 6$ to the duodecaploid, $n = 36$, are represented within the western *Chamaemelanium* violets. Uniformity in regard to basal chromosome number is contrasted with extreme variability in re-

gard to characters of the pistil and stigma, which within other northern hemisphere sections are relatively constant. The strict 6-series of chromosome numbers is mainly limited to the violets of the *Chamaemelanium* section and to a few *Melanium* species. This particular base number, found also in the genus *Hybanthus*, and the great variability in pistils and stigmas are indications that the section is a central and primitive one within the violets.

The *Chamaemelanium* section has its richest development in the topographically and ecologically diversified western North America. In this region it has evolved about 33 taxa, belonging to at least seven polyploid lines of distinct evolutionary sequences. Some of these lines have representatives in the eastern part of North America and in east Asia as indicated in table 1, and one species, the diploid *V. biflora*, $n = 6$, is circumpolar.

The other 17 taxa from western North America belong to seven subsections of three other sections. These sections are: 1. *Melanium*, or the field pansies, with one 17-chromosome southeastern species that has reached Colorado; 2. *Plagiostigma*, which follows a 12-series, $n = 12, 24, 36, 48$; several strictly polyploid groups are augmented by adjunct aneuploid ones, $n = 22, 27, 28$; and 3. *Rostellatae*, characterized by a 10-series, having $n = 10, 20, 40$ chromosomes. The latter three sections are more richly represented in other parts of the world, but the 17 western North American taxa provide a fairly representative sampling of even these sections.

One diploid species of *Chamaemelanium*, *V. purpurea*, $n = 6$, and a diploid species of the *Rostellatae*, *V. adunca*, $n = 10$, have evolved series of ecotypic subspecies that enable them to occupy a nearly complete range of habitats within western North America without changing their chromosome numbers.

Spontaneous interspecific hybrids of *V. purpurea* \times *V. tomentosa*, *V. douglasii* \times *V. quercetorum*, and *V. douglasii* \times *V. praemorsa* ssp. *major* were studied cytologically.

The chromosome numbers of the following species have not previously been counted: *V. scopulorum*, $n = 12$; *V. macloskeyi*, $n = 12$; *V. mc-cabeiana*, $n = 12$; *V. occidentalis*, $n = 12$; *V. palustris* ssp. *brevipes*, $n = \text{ca. } 36-48$, irregular, apparently a hybrid; *V. cognata*, $n = \text{ca. } 27$; and *V. clauseniana*, $n = \text{ca. } 22$.

TABLE 1. SOURCES OF CHROMOSOME NUMBERS IN VIOLA¹

SECTION CHAMAEMELANIUM Ging.

¹ Abbreviations: MSB = M. S. Baker collection numbers, primarily at UC; MSB transplant = Baker's garden at Kenwood, Sonoma Co.; JC = Jens Clausen collection numbers; CIW = Carnegie Institution of Washington garden at Stanford. The state is not indicated for California localities.

SUBSECTION BIFLORAE Clausen

V. biflora L. **n = 6**: Botanical garden material (Clausen, 1926; 1927); unknown (Gershoy, 1928); Japan, below 1500 m (Miyaji, 1929).

V. crassa Makino. **n = 24**: Japan, alpine, above 2700 m (Miyaji, 1929).

V. orbiculata Geyer. **n = 24**: North America (Gershoy, 1932).

V. sempervirens Greene. Tetraploid form, southern. **n = 12**: Santa Cruz Co., S of Boulder Creek; garden transplant from central California (Clausen, 1929). Octoploid form, northern, **n = 24**: Oregon, dry woods, collected by Peck (Gershoy, 1934); southern Oregon, collected by Purdy, 1926 (Gershoy, 1934).

V. rotundifolia Michx. **n = 6**: Unknown, E North America (Gershoy, 1934).

SUBSECTION CANADENSES W. Beckr.

V. canadensis L. **n = 12**: Unknown (Gershoy, 1928; Bold and Gershoy, 1934).

V. ocellata T. & G. **n = 6**: Unknown (Gershoy, 1928); garden transplant from central California (Clausen, 1929).

V. rugulosa Greene. **n = 12**: Botanical garden source as "*V. rydbergii* Greene" (Clausen, 1926; 1927).

V. scopulorum Greene. **n = 6**: MSB V-254 transplant, source unknown.

SUBSECTION CHRYSANTHAE W. Beckr.

V. douglasii Steud. Tetraploid form, southern, **n = 12**: Kern Co., summit of Tehachapi Pass (Clausen, 1929); $\frac{1}{4}$ mi S of Tehachapi Pass, MSB, CIW 5576 fixation; W of Glenville, Keck & Clausen 3187; Santa Clara Co., Arroyo Bayo, Keck & Clausen 4544. Octoploid form, northern, **n = 24**: Sonoma Co., Melita, JC 732; Plumas Co., Indian Valley, MSB 8645 transplant, **2n = 59**, possibly derivative of *V. quercetorum* (MSB 8644, **n = 12**) in same locality; Oregon, Klamath Co., Swan Lake Valley, Applegate 9318, **2n = 48**.

V. douglasii, **n = 12**, \times *V. quercetorum*, **n = 12**: Kern Co., Glenville, Keck & Clausen 3194-2, $6_{II} + 12_{I}$, **2n = 24**; Santa Clara Co., Arroyo Bayo, Keck & Clausen 4546-1, **2n = 24**, metaphase I highly irregular.

V. douglasii, **n = 24**, \times *V. praemorsa* ssp. *major*, **n = 24** ("*V. praemorsa* ssp. *arida*" according to Baker): Oregon, Klamath Co., Swan Lake Valley, Applegate 8319 (DS), **2n = 48**, no pairing in metaphase I.

V. hallii Gray. **n = 36**: Collected by Purdy, April, 1928 (Gershoy, 1932), **2n = ca. 72**.

V. sheltonii Torr. **n = 6**: Nevada Co., Big Ben Ranger Station, MSB 5310 transplant.

SUBSECTION NUDICAULES W. Beckr.

V. alliariifolia Nakai. **n = 6**: Japan (Miyaji, 1929).

V. brevistipulata W. Beckr. **n = 6**: Japan, as *V. glabella* Nutt. (Miyaji, 1913; 1927).

V. eriocarpa Schwein. **n = 6**: E North America (Gershoy, 1928).

V. glabella Nutt. **n = 12**: Garden transplant from central California (Clausen, 1929).

V. kiskidai Nakai. **n = 6**: Japan (Miyaji, 1929).

V. lobata Benth. **n = 6**: Unknown source (Gershoy, 1928).

V. pubescens Ait. **n = 6**: E North America (Gershoy, 1928); Wisconsin, near Madison, in woods (Clausen, 1929).

SUBSECTION NUTTALLIANAE Baker (W. Beckr. pp.)

V. bakeri Greene. **n = 24** (Baker, 1949c) ssp. *bakeri*: Tehama Co., Mt. Lassen National Park, 6000 ft, MSB 8377; Sierra Co., Webber Lake, open forest, 6770 ft, MSB 8388; Nevada Co., W of Big Bend Ranger Station, MSB 5215 transplant; Bear Valley—Bowman Lake Rd., MSB 8406; Placer Co., Road Truckee to Tahoe Tavern, 6100 ft, MSB 8403.

V. linguifolia Nutt. **n = 18**: Idaho, near Moscow, collected by Fisher as "*V. praemorsa*" (Gershoy, 1934); Utah, Cache Co., Brush Canyon, MSB 4465 transplant.

V. nuttallii Pursh. n = 12 (Baker, 1949d): Canada, Alberta, Calgary, *McCalla* 7335; Colorado, nursery plant from Andrews Nursery, *MSB V-279* transplant.

V. praemorsa Dougl. ssp. *praemorsa*. n = 18 (Gershoy, 1934): Washington, S of Tacoma, coastal prairie, *MSB 9634* transplant; Oregon, Josephine Co., Takilma, Purdy nursery stock (Gershoy, 1934); Humboldt Co., Yager, *MSB 4059* transplant.

V. praemorsa ssp. *major* (Hook.) Baker & Clausen. n = 24 (Baker, 1949d): Washington, Kittitas Co., E of Goldendale, *MSB 7386*, region of the type; Idaho, Nez Perce Co., near Cul-de-Sac, *MSB 7399*, type locality of "*V. flavovirens* Poll.;" Idaho Co., Kamiah, N bank of Clearwater River, *MSB 7408*; Oregon, Klamath Co., Swan Lake Valley, with hybrid, *Applegate 8317* (DS); Sierra Co., near Webber Lake, 6700 ft, *MSB 8385*, type of "ssp. *arida* Baker."

V. praemorsa ssp. *oregona* Baker & Clausen. n = 24 (Baker, 1949d): Oregon, Klamath Co., McCullom's Mill on road to Medford, *MSB 8292*; E side of Klamath River, on road to McCullom's Mill towards California, *MSB 8288*; Siskiyou Co., Yreka, *MSB 7354*; Trinity Co., Scott Mt., 5800 ft, *MSB 13139*, mistakenly listed as *V. bakeri* ssp. *shastensis*, n = ca. 24 (*M. A. Nobs*).

V. tomentosa Baker & Clausen. n = 6 (Baker, 1949b): Nevada Co., Cisco-Grass Valley Road, *Pinus ponderosa* forest, 5000 ft, *MSB 8699*.

V. vallicola Nels. n = 6 (Baker 1949d): Utah, Cache Co., N outskirts of Providence, about 5000 ft, *Maguire 16928-8*, as "*V. praemorsa*."

SUBSECTION PEDUNCULATAE Clausen

V. charlestonensis Baker & Clausen. n = 6 (Baker, 1949c): Nevada Charleston Mts., *MSB* transplant; Charelston Mts., Lee's Canyon, *MSB 8673*.

V. pedunculata T. & G. ssp. *pedunculata*. n = 6 (Clausen, 1929): Solano Co., Rockville, 500 ft, *Stebbins 6003* (Stebbins et al., 1963); San Mateo Co., San Bruno Mt., I. & J. M. Webber (Clausen, 1929); Monterey Co., Jolon, 1200 ft, *Stebbins 6019* (Stebbins et al., 1963).

V. pedunculata ssp. *tenuifolia* Baker. n = 6 (Baker, 1949d): San Benito Co., Pinnacles, *MSB 9267* transplant; San Luis Obispo Co., S of Paso Robles, 500 ft, *Stebbins 6018* (Stebbins et al., 1963).

SUBSECTION PURPUREAE Baker

V. purpurea ssp. *atriplicifolia* (Greene) Baker & Clausen. n = 6 (Baker, 1949d): Oregon, Deschutes Co., Bend, *MSB 7414*.

V. purpurea ssp. *aurea* (Kell.) Baker & Clausen. n = 6 (Baker, 1949d): Nevada, near Reno, Hunter's Creek, among rocks and sagebrush, *MSB 8634*.

V. purpurea ssp. *dimorpha* Baker & Clausen. n = 6 (Baker, 1949d): Tehama Co., at entrance to Mt. Lassen National Park, 6000 ft, *MSB 8378*; Child's Meadow, E of Mineral, 5000 ft, *MSB 8379*; Plumas Co., S of Humbug Summit, 6000 ft, *Keck & Clausen 3770*; S of Chaparral, 5000 ft, *Keck & Clausen 3775*.

V. purpurea ssp. *geophyta* Baker & Clausen. n = 6 (Baker, 1949d): Oregon, Klamath Co., 30 mi SE of Lapine, volcanic ash in yellow-lodgepole pine forest, *Keck & Clausen 3707*, type; Lassen Co., near Westwood, among *Pinus jeffreyi* and *Abies concolor*, *Keck & Clausen 3766*.

V. purpurea ssp. *integrifolia* Baker & Clausen. n = 6 (Baker, 1949d): Plumas-Butte Co. line, Humbug Summit, 6500 ft, in *Abies magnifica* forest, *Keck & Clausen 3769*, type.

V. purpurea ssp. *mesophyta* Baker & Clausen. n = 6 (Baker, 1949d): Mariposa Co., Yosemite National Park, Porcupine Flat, 8100 ft, *JC 1098*; Tuolumne Co., Tenaya Lake, 8200 ft, *JC 1099*; above Tuolumne Meadows, 9000 ft, transition to ssp. *xerophyta*, *JC 1100*.

V. purpurea ssp. *mohavensis* Baker & Clausen. n = 6 (Baker, 1949d): San Benito Co., Lockwood Valley, *CIW 1815* transplant; San Bernardino Co., Horse Thief Canyon, 328 ft, *Clokey 5833*, type; 7 mi SE of Hesperia, E side of Mohave River, 3100 ft, *Stebbins 6017* (Stebbins et al., 1963).

V. purpurea ssp. *purpurea*. n = 6 (Baker 1949d): Trinity Co., 35 mi NW of Redding, *MSB* 7427; Tehama Co., near Payne's Creek, 1600 ft, *MSB* 8655; Lake Co., 2.5 mi N of Salmina's Resort, in *Pinus ponderosa* and *Pseudotsuga* forest, 2500 ft, *Stebbins* 6011; Bartlett Mt., 4100 ft, *Stebbins* 6008; Loch Lomond Resort, in *Pinus ponderosa* forest, 2800 ft, *Stebbins* 6022 (Stebbins et al., 1963); Tuolumne Co., Mather, Hog Ranch, 4600 ft, with *Pinus ponderosa*, *CIW* 1015-1 transplant.

V. purpurea ssp. *venosa* (Wats.) Baker & Clausen. n = 6 (Gershoy, 1934): Washington, Kittitas Co., Blewett Pass, 4100 ft, *Keck & Clausen* 3550; near Bingen, collected by *Suksforf* (Gershoy, 1934); Utah, Wasatch Co., Timpanogas Highway, 1 mi E of summit, in aspen grove, *MSB* 8529.

V. purpurea ssp. *xerophyta* Baker & Clausen. n = 6 (Baker, 1949d): Mono Co., Mt. Conness, terraces on E slope, 10400 ft, *JC* 524.

V. quercetorum Baker & Clausen. n = 12 (Baker, 1949): Oregon, Josephine Co., Wimer, *MSB* 9049 transplant; as "*V. purpurea*," collected by *Purdy* (Gershoy, 1934); Plumas Co., Indian Valley, *MSB* 8644; Lake Co., Loch Lomond Resort, 2800 ft, *Stebbins* 6021 (Stebbins et al., 1963); S of Kelseyville, *MSB* 8208; at Lakeview-Knoxville Road, *MSB* 8169, n = 12 + fragment; Napa Co., Howell Mt., Pine Flat, *MSB* 7666 transplant; Howell Mt., near Pacific Union College, 1870 ft, *Stebbins* 5986, 6007 (Stebbins et al., 1963); Marin Co., Mt. Tamalpais, upper limit of forest, *JC* 1178; Contra Costa Co., Mt. Diablo, at summit, *JC* 1172, 1173; Santa Clara Co., Mt. Hamilton, brick kiln on W side, *Keck & Clausen* 4516; Mt. Hamilton, east side, Arroyo Bayo, *Keck & Clausen* 4545, hybridized with *V. douglasii*; Monterey Co., 9 mi NW of Jolon, 1200 ft, *Stebbins* 6020 (Stebbins et al., 1963), near *V. pedunculata*; San Benito Co., 5.4 mi S of Willow Creek School, *CIW* 1816 transplant; Kern Co., at road from Woody to Kernville, to summit, *Keck & Clausen* 3185; W of Glenville, *Keck & Clausen* 3186-1, type locality, hybridizing with *V. douglasii*; Tehachapi Pass, *MSB* 8806.

V. utahensis Baker & Clausen. n = 12 (Baker, 1949b): Utah, Cache Co., Logan Campus, under *Artemisia tridentata*, *Maguire* 16022; mouth of Providence Canyon, under *Artemisia*, *Maguire* 16027-6, type locality; near Providence, under *Prunus*, *Maguire* 16027-7.

SECTION PLAGIOSTIGMA Godr. (NOMINIUM pp.)

SUBSECTION Blandae Gershoy

V. blanda Willd. n = 22 (Gershoy, 1932).

V. incognita Brain. n = 22 (Gershoy, 1932).

SUBSECTION BOREALI-AMERICANAE W. Beckr.

V. clauseniana Baker. n = ca. 22: Utah, Zion National Park, base of Weeping Rock area, *MSB* 8438 transplant.

V. cognata Greene. n = ca. 27: Colorado, Estes National Park, *MSB* transplant.

V. nephrophylla Greene. n = 27 (Gershoy, 1928): Plumas Co., Drakesbad, *MSB* transplant.

16 related species. n = 27: E and central United States (Gershoy, 1929; 1932).

SUBSECTION STOLONOSAE Kupffer

V. epipsila Ledeb. n = 12 (Clausen, 1926; 1927): Denmark, Lyngby.

V. lanceolata L. n = 12 (Gershoy, 1928): Unknown locality.

V. mccloskeyi Lloyd. n = 12: Tulare Co., Mineral King, *MSB* transplant.

V. mocabeaniana Baker. n = 12: Canada, British Columbia, Columbia Lake, *MSB* 9444 transplant, from type locality.

V. occidentalis (Gray) Howell. n = 12: Oregon, Josephine Co., Kerby, *MSB* transplant.

V. pallens (Ging.) Brain. n = 12: (Gershoy, 1928); Unknown locality.

V. palustris × *V. epipsila*. $2n = 36$, $12_{II} + 12_I$: Denmark, forest meadow (Clausen, 1927).

V. palustris ssp. *brevipes* Baker. Irregular meiosis, 36–38 pairs or singles: Colorado, Estes Park, *MSB 7629* transplant.

V. primulifolia L. $n = 12$ (Gershoy, 1928; 1932): E North America.

V. shihokiana Makino. $n = 12$ (Miyaji, 1929): Japan.

SECTION ROSELLATAE Boiss. (NOMINIUM pp.)

SUBSECTION ROSULANTES Borb.

V. adunca Sm. ssp. *adunca*. $n = 10$ (Clausen, 1929): British Columbia, Vancouver, *MSB* transplant; Mendocino Co., Albion, bluffs, *CIW 1828-1* transplant; Marin Co., Mt. Vision (Clausen, 1929); San Mateo Co., San Bruno Mt., collected by I. & J. M. Webber (Clausen, 1929); Montara, *JC 630*, *CIW 1817* transplant.

V. adunca ssp. *ashtona* Baker. $n = 10$: Colorado, Estes Park, Cub Lake Trail, 8500 ft, *MSB 5430* transplant, type locality.

V. adunca ssp. *oxyceras* (Wats.) Jeps. $n = 10$: Oregon, Grant Co., 3 mi W of Dixie Pass, *Keck & Clausen 3659*; Nevada Co., Big Bend Ranger Station, *MSB* transplant; Donner Lake, 7000 ft, *MSB* transplant; Tuolumne Co., Mather, 4600 ft, *CIW 1829-1* transplant.

V. adunca ssp. *radicosa* Baker, (cf. *V. bellidifolia* Greene). $n = 10$: Colorado, Rocky Mountains National Park, Kewuneeche Valley, 12 mi N of Grant Lake, *MSB 4772*, type.

V. howellii Gray. $n = 20$, $n = 40$ (Gershoy, 1928; 1932): tetraploid form, central Oregon, collected by Peck, May 26, 1925 (Gershoy, 1928, " $2n = 42$ "). Octoploid form, Oregon, near Oregon City, collected by Gale, Wildwood Nurseries, Portland, type locality (Gershoy, 1932).

Department of Plant Biology, Carnegie Institution of Washington,
Stanford, California

LITERATURE CITED

- BAIRD, V. B. 1936. A natural violet hybrid. *Madroño* 3:325–327.
 ———. 1942. Wild violets of North America. Univ. Calif. Press, Berkeley.
 BAKER, M. S. 1935. Studies in western violets. I. *Madroño* 3:51–57.
 ———. 1936. Studies in western violets. II. New Species and varieties. *Madroño* 3:232–239.
 ———. 1938. An undescribed species of *Viola* from Utah. *Madroño* 4:194–196.
 ———. 1940. Studies in western violets. III. *Madroño* 5:218–231.
 ———. 1947. A new violet from Mexico. *Madroño* 9:131–137.
 ———. 1949a. A new western violet. *Leafl. West Bot.* 6:101–102.
 ———. 1949b. Studies in western violets. IV. *Leafl. West. Bot.* 5:141–147.
 ———. 1949c. Studies in western violets. V. *Leafl. West. Bot.* 5:173–177.
 ———. 1949d. Studies in western violets. VI. *Madroño* 10:110–128.
 ———. 1953. Studies in western violets. VII. *Madroño* 12:8–16.
 ———. 1957. Studies in western violets. VIII. The Nuttallianae continued. *Brittonia* 9:217–230.
 ———. 1960. Studies in western violets. IX. Miscellaneous species in the sections *Nomimium* and *Chamaemelanium*. *Madroño* 15:199–204.
 BOLD, H. C. and A. GERSHOY. 1934. Studies in North American violets. IV. Chromosome relations and fertility in diploid and tetraploid species hybrids. *Vt. Agr. Exp. Sta. Bull.* 378.
 BRAINERD, E. 1906. Hybridism in the genus *Viola*. III. *Rhodora* 8:49–61.
 ———. 1921. Violets of North America. *Vt. Agr. Exp. Sta. Bull.* 224.
 ———. 1924. Some natural violet hybrids of North America. *Vt. Agr. Exp. Sta. Bull.* 239.

- CLAUSEN, J. 1926. Genetical and cytological investigations on *Viola tricolor* L. and *V. arvensis* Murr. *Hereditas* 8:1-156.
- . 1927. Chromosome number and the relationship of species in the genus *Viola*. *Ann. Bot.* 41:677-714.
- . 1929. Chromosome number and relationship of some North American species of *Viola*. *Ann. Bot.* 43:741-764.
- . 1931a. *Viola canina* L., a cytologically irregular species. *Hereditas* 15:67-88.
- . 1931b. The *Viola* species of Denmark. *Bot. Tidsskr.* 41:317-335.
- . 1931c. Cyto-genetic and taxonomic investigations in *Melanium* violets. *Hereditas* 15:219-304.
- . 1951. Stages in the evolution of plant species. Cornell Univ. Press, Ithaca.
- CLAUSEN, J., R. B. CHANNELL, and U. NUR. 1964. *Viola rafinesquii*, the only *Melanium* violet native to North America. *Rhodora* 66:32-46.
- CLAUSEN, J., D. D. KECK, and W. M. HIESEY. 1940. Experimental studies on the nature of species. I. Effect of varied environments on western North American plants. *Carnegie Inst. Publ.* 520.
- GERSHOY, A. 1928. Studies in North American violets. *Vt. Agr. Exp. Sta. Bull.* 279.
- . 1932. Descriptive notes for *Viola* exhibit. The *Nominium* and *Chamaemelum* section. Sixth Intl. Cong. Genetics, Ithaca, N.Y. (A. Gershoey, *Vt. Agr. Exp. Sta.*, Burlington, 27 pp.)
- . 1934. Studies in North American violets. III. Chromosome numbers and species characters. *Vt. Agr. Exp. Sta. Bull.* 367.
- MIYAJI, Y. 1913. Untersuchungen über die Chromosomenzahlen bei einigen *Viola*-Arten. [In Japanese.] *Bot. Mag. Tokyo.* 27:443-460. (German abstract, *Bot. Mag. Tokyo* 41:262-268. 1927).
- . 1929. Studien über die Zahlenverhältnisse der Chromosomen bei der Gattung *Viola*. *Cytologia* 1:28-58.
- MOORE, D. M. 1959. Population studies on *Viola lactea* Sm. and its wild hybrids. *Evolution* 13:318-332.
- STEBBINS, G. L., B. L. HARVEY, E. L. COX, J. N. RUTGER, G. JELENCOVIC, and E. YAGIL. 1963. Identification of the ancestry of an amphiploid *Viola* with the aid of paper chromatography. *Am. Jour. Bot.* 50:830-839.
- VALENTINE, D. H. 1949. Vegetative and cytological variation in *Viola riviniana*. *Bot. Soc. British Isles, Rep. Conf. Stud. Critical British Groups*, pp. 48-53.

NOTES AND NEWS

NEW DISTRIBUTION RECORD FOR *HELEOCHLOA ALOPECUROIDES* IN OREGON.—Recently Chambers and Dennis (*Madroño* 17:92. 1963) reported on the distribution of *H. alopecuroides* (Pill. & Mitterp.) Host in Oregon. The following record should be included as a range extension of 150 air mi across several mountain ranges and divides to the Rogue River Valley in western Curry Co. about 35 mi from the Pacific Ocean. This is an area which has long been noted for its bizarre and unusual plant records (Baker, *Leaf. West. Bot.* 6:82-84. 1950). The grass was collected on sandy shores along the Rogue River, 3 mi n of Agness, Curry Co. (*Baker 16559*, Aug. 22, 1963, ID, OSC).—WILLIAM H. BAKER, Department of Biological Sciences, University of Idaho, Moscow.